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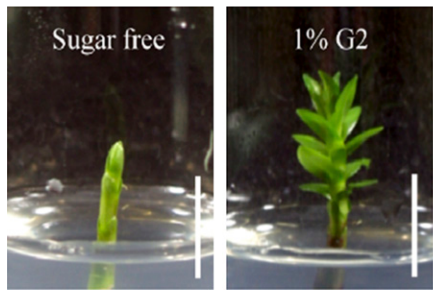
IN BRIEF

Bitter Taste of Winter: Gentiobiose Regulates Overwintering Bud Dormancy in *Gentiana*

It's that time again. Deciduous plants are shedding their leaves in preparation for the long, cold winter ahead. Ornamental perennials such as alpine gentians (*Gentiana*) are busy producing overwintering buds (OWBs), which persist through the cold, snowy winter until the onset of budbreak in the spring. While much is known about the process of seed dormancy, the molecular mechanisms underlying bud dormancy remain obscure. There are two stages of gentian OWB dormancy: endodormancy and ecodormacy. During endormancy, budbreak cannot occur at any temperature. After the required chilling period, OWBs become ecodormant; only cold temperatures prevent budbreak. The freezing tolerance of dormant OWBs has been ascribed to their high levels of stress-related proteins, such as dehydrins. Several potential regulators of bud dormancy have been identified, such as the environmentally regulated *FLOWERING LOCUS T* genes, which appear to inhibit dormancy and induce vegetative growth (reviewed in Horvath, 2009). Phytohormones also play a role in this process; abscisic acid is a negative regulator of dormancy release, while gibberellic acid induces budbreak. In addition, sugars may regulate bud dormancy through interactions with phytohormones. Recent transcriptome and proteome profiling studies of perennial buds have revealed that several metabolic pathways not related to phytohormones are modulated during bud dormancy in various perennials (Bi et al., 2011), indicating that much remains to be learned about this process.

In a pioneering study, **Takahashi et al. (2014)** conducted targeted metabolome analysis of gentian OWBs harvested at early endormancy, early ecodormancy, and late ecodormancy to identify regulators of OWB dormancy. The authors detected a fluctuation in the concentration of gentiobiose, a rare, bitter-tasting disaccharide (named after its first known source, gentian root) that has long been used as a digestive aid. Gentiobiose levels in OWBs peaked during the early and late stages of dormancy but were low during early ecodormancy, a pattern nearly identical to that of glucose but opposite that of the trisaccharide gentianose. This observation led to the speculation that gentianose is hydrolyzed to gentiobiose, which is in turn hydrolyzed to glucose via the activity of glucosidase, providing the energy required for budbreak. However, an increase in this hydrolytic activity was not observed in late ecodormant OWBs, suggesting that gentiobiose is not generally used as an energy source, but instead, there is another reason for gentiobiose accumulation prior to budbreak. Analysis of excised OWBs exposed to chilling treatment helped confirm the correlation between increasing gentiobiose levels and budbreak.



Gentiobiose induces budbreak in vitro. In vitro-grown OWBs cultured on sugar-free or 1% (w/v) gentiobiose (G2) medium for 3 weeks. Bars = 1 cm. (*Reprinted from Takahashi et al. [2014], Figure 6B*.)

To obtain direct evidence for the role of gentiobiose in budbreak, the authors performed a gentiobiose-feeding experiment using in vitro-cultured OWBs. While the OWBs appeared unchanged when cultured on sugar-free medium, those cultured on gentiobiose-containing medium frequently exhibited budbreak (see figure). Gentiobiose treatment induced metabolic changes as well, including increased synthesis of sulfur-containing amino acids as well as ascorbate (AsA) and GSH, two strong antioxidants that detoxify reactive oxygen species through the AsA-GSH cycle. Conversely, depletion of AsA and GSH suppressed gentiobiose-induced budbreak, which was accompanied by reduced redox status. Therefore, gentiobiose appears to act as a signal to break dormancy in gentian OWBs through the AsA-GSH cycle. Much work remains to be done to further elucidate this process and to determine if signaling by gentiobiose or other sugars is a general phenomenon in plants. Indeed, this study opens new avenues of research investigating the nature of signaling and the mechanisms employed by plants to ensure their survival through correct timing of a physiological process.

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